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EDITORIAL

Quantifying Evolutionary Development Using Non-Model Organisms: Integrating Morphology, Metrical Frameworks, and Gene Expression

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ABSTRACT

Keeping pace with the forward progression of evolutionary developmental studies and their trajectory toward ever-more integrative and broad-scale study presents a challenge for researchers from diverse disciplines. Increasing the capacity for discourse and opening opportunity to further interdisciplinary work is highly desirable, and one way that activities can be hindered is through a lack of communication between those developing new methods and those applying methods to new data sets. The goal of this special issue, which brings together contributions from a recent symposium at the 10th International Congress for Vertebrate Morphology (ICVM 10, Barcelona, July 2013) along with select additions, was to integrate methodological developments with molecular and morphological data to present a broad spectrum of avenues for investigating ontogeny in land vertebrates. A balance between methods-focused papers and papers presenting novel data and perspectives from molecular and morphological approaches in evo-devo was sought with the hope of promoting greater interchange between each side, and drawing attention to new opportunities for future research on non-model organisms. *J. Exp. Zool. (Mol. Dev. Evol.) 322B:555–557, 2014.* © 2014 Wiley Periodicals, Inc.

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Stemming from traditional comparative embryology, the field of evolutionary developmental biology ("evo-devo") originated in the 1970 s and 1980 s and has attracted growing interest through novel and fruitful interactions between evolutionary biologists and developmental biologists. Since its inception, evo-devo has inspired refinement and reconsideration of traditional conceptual backgrounds (Olsson et al., 2006; Pigliucci and Müller, 2010; Asher and Müller, 2012). The overarching aim to uncover generative mechanisms underlying biological diversity has supported and united a broad spectrum of research avenues that continue to expand in pace with technological advance-

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ments in molecular biology and the improvement of quantitative tools. The latter, together with recent progress made in high-resolution embryonic imaging techniques, has widened the focal frame of evo-devo studies to include an array of non-model species.

As a result, a body of literature has amassed on patterns of evolutionary development for many taxa, and a number of algorithms have been used to tackle the problem of extracting quantifiable variables to test hypotheses within a phylogenetic framework. Among those are methods to study sequence heterochrony, changes in the relative timing of developmental events, in addition to advanced ordination and transformation methods to study allometry. Both heterochrony and allometry have a long history (Klingenberg, '98; Urdy et al., 2013) and recent revitalized interest in those frameworks has stemmed from the recognized power of partnering new methods with increased taxonomic sampling to address macroevolutionary questions (e.g. Goswami et al., 2014). These include the sampling of rare taxa to shed light on the developmental patterns of previously unstudied groups, as well as identifying features of development that distinguish major clades, contrasting for example placental and marsupial mammals (e.g. Sears, 2004; Sánchez-Villagra et al., 2008; Weisbecker et al., 2008) or "northern" (Laurasiatheria and Euarchontoglires) and "southern" (Afrotheria and Xenarthra) placentals (Hautier et al., 2013).

Keeping pace with the forward progression of evolutionary developmental studies and their trajectory toward ever-more integrative and broad-scale study presents a challenge for researchers from diverse disciplines. Increasing the capacity for discourse and opening opportunity to further interdisciplinary work is highly desirable, and one way that activities can be hindered is through a lack of communication between those developing new methods and those applying methods to new data sets. A wish to improve upon this issue provided impetus for a recent symposium at the 10th International Congress for Vertebrate Morphology (ICVM 10, Barcelona, July 2013), in which we aimed to integrate conceptual developments with molecular and morphological data to present a broad spectrum of avenues for investigating ontogeny in land vertebrates, and to stimulate increased communication between members of each field. This special issue of the Journal of Experimental Zoology, Part B, brings together contributions from participants of that symposium along with select additions, these comprise morphological (Hautier and colleagues, Koyabu and Son, Schoch) and molecular (Sears) approaches to evo-devo research, introductions to novel methods for the use of quantitative data in the frameworks of heterochrony and allometry (Laurin, Giannini), as well as a timely review of methodological advancements (Ziermann and colleagues). Our goal was to find a balance between methods-focused papers and papers presenting novel data and perspectives from molecular and morphological approaches with the hope of promoting greater interchange between each side, and drawing attention to new opportunities for future research on non-model organisms.

For the methods-focused half of the issue, advancements in the study of allometry and heterochrony are presented together with worked examples of their application to developmental data on a macroevolutionary scale. Giannini introduces a novel approach to map multivariate allometric coefficients onto a phylogeny by dealing with those as continuous characters. Using an optimization method that is straightforward to implement in freely available software, Giannini provides a way to reliably reconstruct ancestral allometric patterns, identify nodes on a phylogeny that correspond to particular shifts in allometric patterns, and assess the association of other characters (e.g. body mass) to allometric coefficients. The vast literature on ontogenetic allometry for a wide range of taxa contains data that are directly amenable to this approach, and its potential is further underlined by the capacity to project back into the evolutionary history of a lineage, allowing for a deep-time perspective on the evolution of ontogeny. In a similar vein, Laurin expands upon the pathways to analyze ontogenetic data by exploring the possibility of identifying developmental modules (units composed of highly connected traits) using ossification sequence data. Ossification data for the cranium and/or postcranium have been used extensively to identify sequence heterochronies in a number of clades, but the link between heterochrony and modularity, namely that for shifts in developmental events to occur there has to be some autonomy (i.e. modularity) of the traits involved, has yet to be fully explored. Laurin sets out a series of tests to identify or generate hypotheses about the presence of modules, and this approach holds broad significance for evo-devo workers by providing a bridge towards functional- or evolutionary-based hypotheses of modularity at molecular and morphological levels. Ossification sequence data have more frequently been analyzed using sequence heterochrony methods and, as discussed by Ziermann and colleagues in this volume, although there are a number of possible approaches those each come with merits and drawbacks. Using an extensive, novel data set on larval cranial musculature development in anurans, Ziermann and colleagues provide important insights into the role of heterochrony in early developmental events as well as delving further into the issues surrounding character non-independence, and the choice of phylogenetic framework and its impact on recovering heterochronic shifts.

The link between any uncovered inter-specific variation in sequences of developmental events and life-history parameters is not well understood and often lacking, as Ziermann and colleagues discuss with their cranial musculature data. Koyabu and Son treat this aspect in more detail in their study of postcranial ossification sequences in bats, which along with contributions by Hautier and colleagues, Schoch, and Sears, represents the complementary half of the issue, where the focus shifts towards exploration and discussion of novel data. Koyabu

and Son discuss the potential relation between locomotive mode and skeletogenesis and consider how heterochronic shifts found in bats, and absent in other terrestrial boreoeutherian species, may reflect the demands of powered flight. These data complement molecular work on innovations underlying forelimb development in bats and on the link between functional adaptation and heterochrony. Schoch, in this volume, also assesses developmental patterns within a functional-adaptive context. By constructing growth trajectories for skull bones of frogs and salamanders from fossil ossification sequences and integrating those with developmental data from extant representatives, Schoch's approach exemplifies the strengths of a deep-time narrative to development in revisiting the question of the origin of the extant amphibian skull. Rather than focusing on heterochrony, Schoch instead concentrates on heterotopy, an alteration in the spatial arrangement of a structure, and its role in skull element organization in the evolution of the amphibian skull. Hautier and colleagues, in this volume, also focus on skeletogenesis. They approach skeletal development using microtomography techniques, illustrating the high level of detail that can be obtained using non-invasive methods. Their study is the first to detail vertebral ossification sequence at an individual element scale in wildtype and mutant mice. Hautier and colleagues relate their findings to Hox and Cdx gene expression patterns in the axial skeleton of mice, and the results provide a baseline against which to consider the diversity of axial skeletal morphology in mammals. The data provided by Hautier and colleagues are important for testing mechanisms proposed to be behind the low level of variation observed in vertebral counts in mammals, an active area of research particularly exploring the nature of developmental constraints. While Hautier and colleagues touch on the topic of developmental constraints briefly, Sears' contribution to this volume deals in more depth with developmental constraints in mammalian evolution and provides an overview of how development affects the trajectory of phenotypic evolution. By delving into more details on the theoretical underpinnings of evo-devo, Sears presents a timely insight into the diversity of possible investigative-pathways for studying the evolution of development. Sears selects a number of recent, important studies to highlight that the way development shapes morphogenesis is system-specific, and that evo-devo may benefit from further study being directed towards non-model systems, clarifying how the distribution of population-level variation is related to (determined by) developmental processes and in turn how the variation at the population-level equates to phenotypic evolution on a macro scale. The take home message, that evo-devo has matured to be a diverse and exciting discipline with much future promise, is one that we hope is seen in all the contributions and authors' research areas covered here.

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